Ethology Ecology & Evolution, 2014
Vol. 26, No. 4, 349–364, http://dx.doi.org/10.1080/03949370.2013.851121

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Life-history theory predicts host behavioural responses to experimental brood parasitism

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Received 27 November 2012, accepted 26 September 2013

Life-history theory posits that the evolutionary responses of hosts to avian brood parasitism will be shaped by the extent of the fitness costs of parasitism. Previous modelling work predicted that hosts of more virulent parasites should eject foreign eggs, irrespective of clutch size, whereas hosts of less virulent parasites, with smaller clutch sizes, should desert (abandon) parasitized clutches and, with larger clutch sizes, should eject foreign eggs. Egg rejection behaviour of European blackbirds (*Turdus merula*) and song thrush (*T. philomelos*) in their introduced range in New Zealand was induced by manipulating the colour of one of the birds' own eggs. We also used parallel experimental manipulations in the common redstart (*Phoenicurus phoenicurus*), a regular host species with a large clutch size which pays a moderate cost when parasitized by the common cuckoo (*Cuculus canorus*). In all three species, eggs coloured entirely black were more often rejected than eggs coloured with black spots but with the rest of the background colour left visible. Rejections of black eggs occurred mainly through nest desertion in blackbirds, which have smaller clutch sizes, and mainly through egg ejection in song thrush, which have larger clutch sizes. As predicted, redstarts mostly ejected black eggs. Alternative egg rejection behaviours may have evolved in response to differently virulent brood parasitism across these species. For example, in the absence of interspecific parasitism in both their native and introduced ranges, selection by low-cost intraspecific brood parasitism may explain the experimentally-induced behavioural differences in egg rejection in blackbirds, with smaller clutch sizes, versus song thrushes, with larger clutch sizes. Such experimental approaches, informed by life-history theory,

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should be generally useful in larger-scale, comparative frameworks, to determine the relative roles of intra- versus interspecific brood parasitism in the evolution of egg rejection behaviours across diverse avian lineages.

KEY WORDS: brood parasitism, clutch size, life-history theory, nest abandonment, virulence.

INTRODUCTION

Avian brood parasites lay their eggs into other birds' nests, and vary dramatically in the extent to which they reduce the reproductive success of their hosts (DAVIES 2000; KILNER 2005). For example, *Cuculus* cuckoos and other highly virulent parasite chicks typically eliminate all of a host's breeding success by evicting eggs or nestlings soon after hatching (KLEVEN et al. 1999; ANDERSON et al. 2009; but see GRIM et al. 2009a). In contrast, less virulent *Molothrus* cowbirds and intraspecific brood parasite chicks often develop with host nest mates (KILNER et al. 2004). As an evolutionary response to reduce, or to eliminate, the varying costs of avian brood parasitism, potential hosts may avoid parasitism by nesting secretively or attacking adult brood parasites, or may reject parasitism by ejecting foreign eggs and chicks from nests or by deserting (abandoning) parasitized broods to initiate a new breeding attempt elsewhere (DAVIES 2011; KILNER & LANGMORE 2011). However, egg hatching failure (ØIEN et al. 1998) and unsuccessful nest mate eviction (GELTSCH et al. 2012) by the parasite, which are both documented in nests parasitized by cuckoos, allow for some host breeding success even in parasitized broods.

Throughout the global distribution of the thrush genus *Turdus*, several species are regularly impacted by brood parasites, including more virulent *Cuculus* cuckoos (HONZA et al. 2005) and less virulent *Molothrus* cowbirds (FRIEDMANN 1929; ROTHSTEIN 1982; LICHTENSTEIN 1998). *Turdus* thrushes are also occasionally parasitized by conspecifics, which is a lower-cost, less virulent, form of brood parasitism (GRIM & HONZA 2001; MOSKÁT et al. 2003). Previous work on European blackbirds (*T. merula*; hereafter: blackbird) and song thrush (*T. philomelos*) documented variable rejection rates in response to foreign (natural or experimental) eggs of heterospecifics or conspecifics (HALE & BRISKIE 2007; HONZA et al. 2007; GRIM et al. 2011). Specifically, blackbirds were reported to reject non-mimetic model common cuckoo (*Cuculus canorus*, hereafter: cuckoo) eggs at higher rates in some woodland areas of sympatry with the cuckoo compared to nearby urban areas of allopatry in continental Europe (MOSKÁT et al. 2002; but see GRIM et al. 2011). Comparisons of blackbirds and song thrush in areas of sympatry with the cuckoo, including Britain (DAVIES & BROOKE 1989) and the Czech Republic (GRIM & HONZA 2001), and in areas of allopatry in New Zealand (exotic population introduced from Britain: HALE & BRISKIE 2007; SAMAŠ et al. 2011), showed consistently high rejection rates of non-mimetic eggs (reviewed in Table 1 of POLAČIKOVÁ & GRIM 2010). In contrast, with respect to mimetic (natural conspecific or artificially painted) eggs, rejection rates of experimental brood parasitism by blackbirds and song thrush were relatively low in Europe (DAVIES & BROOKE 1989; MOSKÁT et al. 2003; HONZA et al. 2007; GRIM et al. 2011) and variable in New Zealand (BOULTON & CASSEY 2006; HALE & BRISKIE 2007).

One possible explanation for these combined patterns is that the variability and population differences in foreign egg rejection in blackbirds and song thrush are due to a relatively weak evolutionary selection pressure by brood parasitism of low overall virulence. Accordingly, natural parasitism on *Turdus* species in Europe by the cuckoo is very rare (Møller 1976; Grendstad et al. 1999), there are no cuckoo eggs which mimic thrush eggs (Moksnes & Røskaft 1995), and cuckoo chicks are unable to successfully evict and outcompete host nest mates in the deep cup nests of some thrushes (Grim 2006a, 2006b; Grim et al. 2011). Interspecific brood parasitism on *Turdus* thrushes is altogether absent in New Zealand (Hale & Briskie 2007), yet the introduced thrush populations still reject foreign eggs at high rates (Samaš et al. 2011). However, such interpretations can be coarse and inexact, overlooking counterintuitive interactions and feedbacks between diverse life-history traits (Stearns 1992). For example, detailed mathematical modelling of avian host-parasite interactions predicts that based on (1) the extent of phenotypic similarity between host and parasite eggs, (2) the cost of host reproductive investment per breeding bout, (3) the reduction in relative breeding success owing to parasitism (i.e., parasite virulence) and (4) the rate of parasitism, hosts may evolve different rejection behaviours in response to brood parasitism (Reeve 1989; Takasu et al. 1993; Brooke et al. 1998; Servedio & Lande 2003). Specifically, a mathematical model (Servedio & Hauber 2006) using flexible egg recognition mechanisms based on host-parasite egg phenotype discrimination (Hauber et al. 2006) predicted that hosts of more virulent parasites would evolve to reject parasitism predominantly by the method of ejecting foreign eggs from clutches, irrespective of clutch size. In contrast, hosts of less virulent parasites, with smaller clutch sizes, would evolve to desert parasitized clutches, compared to hosts with larger clutch sizes which would eject parasitic eggs (Servedio & Hauber 2006). Comparative data are largely consistent with these predictions of egg rejection methods across hosts of several avian brood parasite lineages: hosts of *Cuculus* cuckoos typically eject parasitic eggs, irrespective of clutch size (Soler et al. 1999; Langmore et al. 2005), whereas hosts of *Molothrus* cowbirds typically desert parasitized nests (Hosoi & Rothstein 2000; Hauber 2003a). Similarly, large-clutch laying Eurasian magpie (*Pica pica*) hosts of the moderately virulent, nest mate-tolerant great spotted cuckoo (*Clamator glandarius*) typically eject the parasitic eggs (Soler et al. 2001), as predicted by the model.

In New Zealand, where we performed our main experiment on the two species of *Turdus* thrushes introduced from the United Kingdom, the clutch size of blackbirds (mode: 3 eggs) is smaller than that of song thrush (mode: 4 eggs; for statistical comparisons, see Cassey et al. 2005; Evans et al. 2005; Samaš et al. 2013a). Accordingly, all else being equal, the Servedio & Hauber (2006) model predicts that less virulent parasitism would select for *more frequent nest desertion in blackbirds* compared to *more frequent egg ejection in song thrush* (Table 1). For example, under the same set of parameter values regarding the fitness value of re-nesting attempts, which is likely to hold true for sympatric thrushes with similar lengths of nesting seasons and shared

Table 1.

Predictions for the mode of rejection behaviours of *Turdus* species from life-history theory modelling (Servedio & Hauber 2006).

Virulence (cost of parasitism)	Clutch size: lower blackbird	Clutch size: higher song thrush
Lower	Desert nest	Eject egg
Higher	Eject egg	Eject egg

predation regimes (Cassey et al. 2010; Samaš et al. 2013a) a clear switch point, from nest desertion to egg ejection, is estimated by the model to fall between species with clutch sizes of 3 versus 4 eggs (Figure 4b in Servedio & Hauber 2006). Alternatively, more virulent brood parasitism is predicted to consistently select for only egg ejection in both species, irrespective of clutch size (Hauber 2003a).

We tested these predictions by colouring one of the hosts' own eggs (Hauber et al. 2006; Moskát et al. 2010; Bán et al. 2013); altering the appearance of a host egg leaves the clutch size in the manipulated nest unchanged, as if a parasite removed one host egg when she laid her own egg (Latif et al. 2006). This was appropriate because the Servedio & Hauber (2006) simulation also assumed replacement, rather than addition, of a host egg with the parasitic egg. These thrush species are suitable subjects for such an experimental test of life-history theory because both nest desertion and egg ejection are known to be components of the behavioural repertoires of the blackbirds and song thrush (Grim & Honza 2001; Moskát et al. 2003; Grim et al. 2011), including in their introduced range in New Zealand (Samaš et al. 2011). Importantly, the introduced populations of both blackbirds and song thrush we studied are currently free of interspecific brood parasitism (Hale & Briskie 2007), and do not suffer from any reduced genetic variation (Briskie & Mackintosh 2004; Congdon & Briskie 2010), perhaps because of repeated introduction events and the large number of individuals (introduction 'propagule pressure' sensu Lockwood et al. 2005) introduced each time (Thomson 1922).

We also used parallel experimentation with a third species to test the general suitability of our research approach; this assured us that any results yielded by our theoretically motivated, experimental manipulations would be interpretable in the context of the avian host-parasite co-evolutionary ecology framework outlined above. Specifically, we chose a species which conformed to the following four criteria: (1) regular host of an interspecific brood parasite, (2) variable cost of parasitism experienced by this host species, (3) documented behavioural flexibility in response to experimental parasitism and (4) naturally exposed to brood parasitism (i.e., sympatry in the native ranges). Parallel experimental work on a species matching these criteria would specifically allow us to test the directional prediction of the Servedio & Hauber (2006) model, regarding the type of behavioural response shown to experimentally colouring birds' own eggs. Accordingly, we studied the common redstart (*Phoenicurus phoenicurus*; hereafter: redstart), parasitized frequently by the common cuckoo in their native European, sympatric ranges. At our study site in southeastern Finland (Grim et al. 2009a, 2009b), this host accepts the highly mimetic eggs of the local cuckoo gens (Avilés et al. 2005; Avilés 2008; Igic et al. 2012). Uniquely among cuckoo hosts, redstarts pay a low cost for cuckoo parasitism in the nest, because parasitic hatchlings routinely fail to evict some or all host nest mates in the cavity-nest of this host, and up to half of the cuckoo chicks perish while competing for parental provisions with host nest mates (Rutila et al. 2002; Grim et al. 2009b). The redstart is a host species which is known to respond with behavioural variability to experimental parasitism; data from this species already confirm some of the predictions of the Servedio & Hauber (2006) model in that introducing model cuckoo eggs in areas of sympatry with the cuckoo (higher cost of parasitism), induced predominantly egg ejection, whereas in areas of allopatry (no cost of parasitism), foreign eggs were predominantly deserted (Rutila et al. 2006). Given that our study was conducted in an area of cuckoo-redstart sympatry (Grim et al. 2009a, 2009b) and, further, this host lays a large clutch size (mode: 6 eggs; Rutila et al. 2002), the Servedio & Hauber (2006) model specifically predicts the rejection of foreign eggs by ejection in this host-parasite system.

Although our three study species are diverse in their distributions, life-history traits, and rates of exposure to parasitism, in the SERVEDIO & HAUBER (2006) model, the critical parameter regarding egg ejection versus nest desertion (nest abandonment) was the relative fitness value of the re-nesting attempt after a nest was deserted due to parasitism. Both species of *Turdus* and the redstarts are similar to each other in that they will readily re-nest after the first clutch has failed during the laying or incubation phase (AVILÉS et al. 2005; CASSEY et al. 2010). Our empirical data show that there is no difference between European (native) and New Zealand (introduced) thrushes (both *T. merula* and *T. philomelos*) regarding (1) egg rejection rate, (2) the repeatability of egg rejection, (3) latency to rejection and (4) the repeatability of the latency to rejection (SAMAŠ et al. 2011). This confirms that both the European and the New Zealand populations of these species are equally suitable for our experiments. Finally, although our study here is based on the experimental comparison of just three species, this work's value lies in providing experimental data additional to prior data based on similar experiments (e.g., HAUBER et al. 2006; MOSKÁT et al. 2010) and to generate more species-specific data for future meta-analyses of comparative patterns of anti-parasitic behavioural responses (e.g., HAUBER 2003a).

METHODS

General procedures

To document behavioural tactics of egg rejection in response to experimentally manipulated shell colours, we searched for *Turdus* nests during the laying and incubation stages to alter the appearance of one of the eggs already laid in a clutch. We collated experimental data from the 2005–2006, 2006–2007, and 2007–2008 austral breeding seasons. Introduced European blackbirds and song thrush are widespread across New Zealand, and occur sympatrically at high densities (CASSEY et al. 2008; SAMAŠ et al. 2013a). Our study sites included urban and rural parkland within a 50-km radius of Auckland and Hamilton cities, North Island, New Zealand (for site and methodological details, see SAMAŠ et al. 2011, 2013a). Each active nest was included in a single experimental procedure. Although breeding birds were not individually colour-marked in this study, pseudo-replication was considered to be minimized by conducting experiments typically within periods of 1–2 weeks at each site, followed by a move to another study site 7+ km away, thus reducing the chance of using two nests of the same parents (thrushes are highly philopatric both within and between breeding seasons: SAMAŠ et al. 2013b). Because we also did not know whether we experimented on first or later clutches, following successful or failed nesting attempts, we included month of year as a co-variate in our analyses (see section on Statistical analyses below).

For our parallel work on a known host of an interspecific brood parasite in its native range, we also located active nests during the laying and incubation stages of redstarts breeding in artificial nest boxes in southeastern Finland, an area of heavy cuckoo parasitism on redstarts, during the 2008 breeding season (for site and methodological details, see GRIM et al. 2009a, 2009b).

Egg manipulation protocols

At each nest, we marked all eggs already in the nest on the blunt pole for individual identification with a black Sharpie® permanent marker felt pen (this numbering per se has no effect on host responses to eggs; POLAČIKOVÁ et al. 2013). In addition, one egg was manipulated with the same pen by randomly either (1) dotting it with 20 black spots of approximately 4 mm in diameter, leaving some of the background colour clearly visible, or (2) colouring it all black, covering the background colour entirely (Fig. 1). We used the 20-spot spot treatment as a control treatment and the black colouring as the experimental treatment, to manipulate each clutch by altering the appearance of one of the bird's own eggs using a consistent brand of marker pen (its colour and scent), but leaving some (20-spot) or covering up all (black) exposure to alter the egg's natural background coloration. In a previous experiment, a 20-spot-like treatment did not significantly alter the egg ejection rate of own eggs by another known cuckoo host, the great reed warbler (*Acrocephalus arundinaceus*), relative to handled, but non-coloured, control host eggs (Hauber et al. 2006). Our parallel set of manipulations in Finland, also included colouring one redstart egg per clutch, either (1) dotted with 12 black spots (the redstart eggs are smaller than *Turdus* eggs), or (2) fully black.

These manipulations perceivably altered the reflectance spectra of the *Turdus* eggshell surface (demonstrated by predictive avian visual modelling: Igic et al. 2009), within the avian-perceivable light wavelengths (Honza et al. 2007; Cassey et al. 2008; Fig. 1). Following the manipulation, each egg was returned to the clutch. This procedure avoided the use of artificial-egg construction materials (Martin-Vivaldi et al. 2002) by manipulating the phenotype of the hosts' own eggs (Hauber et al. 2006), therefore varying specific parameters of egg appearance

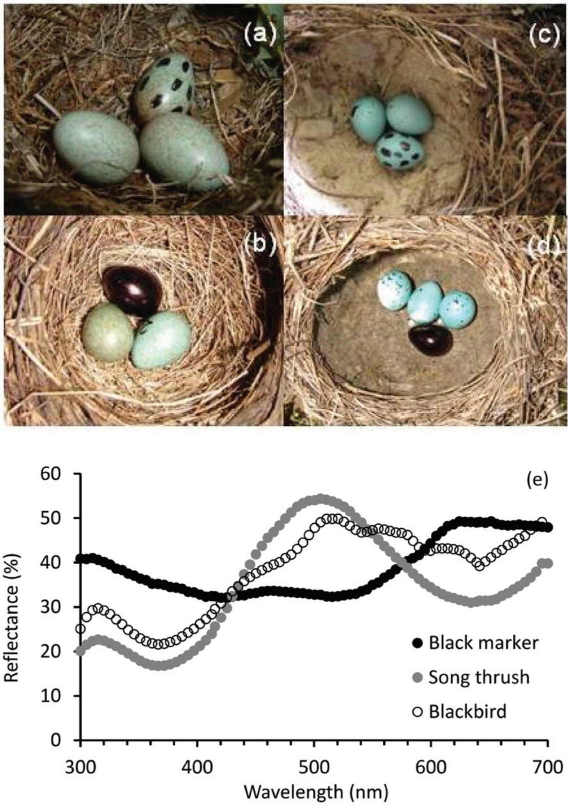

Fig. 1. — Representative clutches with examples of differently manipulated own eggs of (a, b) European blackbirds (*Turdus merula*) and (c, d) song thrush (*T. philomelos*). Representative reflectance spectra (e) of black coloured areas of the eggshell, blackbird egg background, and song thrush egg background (using Ocean Optics HR2000 Miniature Fibre Optic Spectrometer illuminated by a DT mini-lamp; for methods, see Igic et al. 2009).

(maculation or coloration) (Moskát et al. 2008; Bán et al. 2013), but not eggshell thickness (Antonov et al. 2009; Igic et al. 2011).

We acknowledge that no cuckoo host or cuckoo gens lays a purely black egg. However, our manipulation of using a species' own maculation colour (in this case, the black spotting of song thrush eggs), to dye the entire surface of the egg was both (1) successfully employed previously (e.g., Hauber et al. 2006; Samaš et al. 2012) and (2) similar to the majority of prior experiments conducted on cuckoos in that our experimental eggs presented hosts with a stimulus of a single-colour egg with no spotting (Davies & Brooke 1989; Polačiková & Grim 2010), even though none of those many host species tested with such a model egg are parasitized with such a cuckoo egg type naturally (Davies & Brooke 1989; Grim et al. 2011). Finally, interspecific brood parasites typically remove a host egg when laying their own egg (cuckoo: Wyllie 1981, cowbird: Hauber 2003b), and so our protocol replicated natural patterns in that it did not alter the total clutch size in these experiments. In addition, many cuckoo hosts, including blackbirds and song thrush, respond to foreign eggs similarly, irrespective of the removal or non-removal of one of their own eggs (Davies & Brooke 1989).

We monitored nest contents for up to 5 days after manipulation to assess whether the manipulated egg was present or missing (following the criteria of Hale & Briskie 2007). Clutches in which a new egg(s) appeared after the manipulation, were considered to be during the laying stage for the experiment, whereas all other clutches were considered to be during the incubation stage. Eggs that disappeared in ≤ 5 days (experiment = day 0) were considered ejected and clutches with cold or wet eggs during two subsequent visits within the same period were considered deserted. All nests with evidence of predation (i.e., broken eggs, shell remains within a cold clutch, and entirely missing clutch contents) were excluded from the study (Samaš et al. 2013a).

Because nest desertion may not always be a specific response to parasitism (Kosciuch et al. 2006), we used data from unmanipulated *Turdus* nests (i.e., nests that were not included in the experimental group) in the 2007–2008 New Zealand breeding season to assess background levels of desertion. We located and monitored these nests in the same manner as experimental nests but we did not manipulate egg phenotypes except for the numbering of eggs on the blunt pole as described above. These nests were a random sample from the same population of nests.

Statistical analyses

For the *Turdus* data set, we first used logistic regression models (SAS v. 9.3) to examine differences in experimental binary outcome (0 = reject, including both ejection and desertion; 1 = accept) between potential confounding variables year (nominal variable), study sites (n = 3), breeding stages (laying or incubation), and month of nesting (continuous variable). In the absence of an overall statistical effect of these predictors (Table 2), we also pooled the data across these variables and specifically examined whether there were species-specific differences in (1) the effects of egg treatment on the binary response (0 = reject; 1 = accept) or (2) the detailed rejection responses (ejection of manipulated egg versus desertion of entire clutch) between the two *Turdus* species using contingency analyses (Statview v. 5.0.1). We also conducted contingency analyses for the redstart results. Our data set for these *Turdus* species comprises one of the most extensive datasets using the same experimental methodology for foreign egg rejection studies (n = 27–34 per species per treatment) in any two species of passerine congeners (Grim 2007). All tests were two tailed with α = 0.05.

RESULTS

Logistic regression analysis showed no consistent relationships between the binomial outcome of our experiments and four potential confounding variables (year,

Table 2.

Univariate Type III results from logistic regression analyses (for European blackbirds and song thrush, separately) between the binary experimental outcome (0 = reject, 1 = accept) and four potential confounding variables (traits). Estimates are probabilities of accepting the manipulated egg for incubation, logit transformed (with delta method standard errors, SE) from the linear Least Square Mean estimates.

Trait	Species	Blackbird (*Turdus merula*)				Song thrush (*T. philomelos*)			
	Level	Estimate	SE	*F*	*P*	Estimate	SE	*F*	*P*
Year	2005	0.600	0.162	0.12	0.89	0.750	0.158	0.04	0.96
	2006	0.667	0.164			0.700	0.150		
	2007	0.562	0.130			0.700	0.086		
Month	September	0.333	0.285	1.55	0.23	0.750	0.158	0.06	0.94
	October	0.500	0.123			0.690	0.089		
	November	0.786	0.115			0.727	0.139		
Site	Auckland	0.600	0.132	2.40	0.11	0.692	0.132	0.02	0.98
	Hamilton	0.786	0.115			0.727	0.139		
	Tawharanui	0.167	0.159			0.708	0.096		
Stage	Laying	0.625	0.102	0.19	0.67	0.714	0.087	0.01	0.92
	Incubating	0.545	0.155			0.700	0.105		

month, site, stage) for either species (Table 2). Blackbirds rejected the black egg more often than the spotted egg (logistic regression, $t = 2.42$, $P = 0.021$; Fig. 2). Song thrush also rejected the black egg more often than the spotted egg ($t = 2.83$, $P = 0.007$; Fig. 2).

In response to the spotted egg manipulation, some blackbirds ejected spotted eggs and did not desert nests, and some song thrush either ejected spotted eggs or deserted nests (Fig. 3). However, there was an overall low rate of rejection following this manipulation in the two *Turdus* thrushes (< 20%, Fig. 2), and sample sizes were too small to statistically test for a difference in the behavioural mode of rejection between

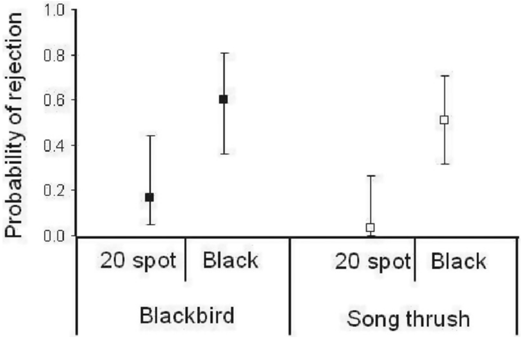

Fig. 2. — Outcomes of experiments in European blackbird (*Turdus merula*) and song thrush (*T. philomelos*) clutches in response to the colour manipulation of single own eggs. The probabilities of the rejection (egg ejection and nest desertion combined) of experimentally manipulated own egg are estimated by Least Square Means (and their standard errors), and shown for each species and treatment.

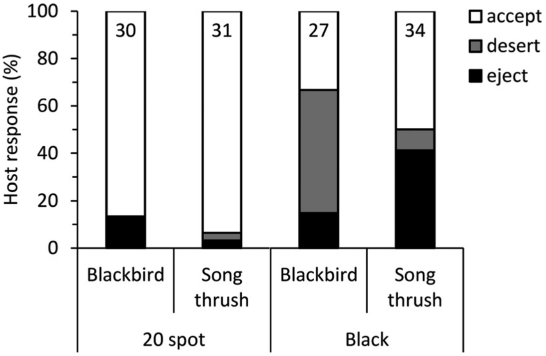

Fig. 3. — Detailed behavioural responses (egg acceptance, nest desertion or egg ejection) of European blackbirds (*Turdus merula*) and song thrush (*T. philomelos*) in response to colour manipulation of a single own egg per clutch. Sample sizes are given within bars.

the two thrush species following the spotted treatment. In contrast, following the black egg treatment, rejection responses were common in both species, but blackbirds more often deserted nests with the black egg, compared to song thrush, whereas song thrush more often ejected black eggs than did blackbirds (Fisher's exact test [FEt]: $P = 0.0006$; Fig. 3).

Nest desertion in the non-manipulated nests of the blackbird (5 of 22: 23%) was in fact higher than desertion of experimental nests with the spotted egg (0 of 30: 0%; FEt: $P = 0.01$). Similarly, nest desertion in the song thrush nests was higher in the non-manipulated (6 of 23: 26%) than in the spotted egg treatment (1 of 31: 3%; FEt: $P = 0.034$). In contrast, nest desertion was higher in the blackbird nests with the black egg (14 of 27: 52%) than in non-manipulated nests (23%; FEt: $P = 0.045$), and statistically similar in song thrush nests with the black egg (3 of 34: 9%) to that of the non-manipulated nests (26%; FEt: $P = 0.14$).

In the spotted manipulation with redstarts, 16 (94%) hosts accepted spotted eggs and 1 (6%) deserted the nest; no eggs were ejected. In the black egg treatment, 10 (45.5%) accepted the spotted egg, 10 (45.5%) hosts ejected the black egg, and 2 (9%) deserted the nest. The difference between the behavioural outcomes of the two treatments was statistically significant overall ($\chi^2 = 13.8$, $P = 0.01$). As predicted, redstarts rejected black eggs more often by ejection (83%) than by desertion (17%; binomial test, $P = 0.039$).

DISCUSSION

Our data support previous work on blackbirds, song thrush and most other hosts of brood parasites in that they demonstrate that experimental eggs whose background coloration matches the hosts' own eggs are more likely to be accepted than eggs whose background coloration is altered dramatically (ROTHSTEIN 1975; DAVIES & BROOKE 1989; MOSKÁT et al. 2003, 2008; HAUBER et al. 2006). The methodological suitability of our approach to induce egg rejection behaviours in potential hosts of interspecific brood parasites was also confirmed by our parallel experiments with the redstart, a known current host of the cuckoo, that responded to black eggs by ejection significantly more so relative to the spotted egg treatment. However, all of our manipulations also exposed hosts to different amounts (i.e., less: 20 spot; more: black) of olfactory cues, emanating from the use of marker pen ink, and so some individuals may have based their rejection responses on scent variation between the differently manipulated eggs (although there is no empirical support for this speculation in any host of brood parasites yet). Nonetheless, our study's main conclusions below are based on the variable behavioural patterns of host rejection responses to different sets of manipulations and across multiple species, irrespective of whether visual, olfactory or other cues triggered the rejection responses.

In contrast to previous work on *Turdus* species in both their native (GRIM & HONZA 2001; MOSKÁT et al. 2003; HONZA et al. 2007; POLAČIKOVÁ & GRIM 2010; GRIM et al. 2011) and introduced ranges (HALE & BRISKIE 2007; SAMAŠ et al. 2011; POLAČIKOVÁ et al. 2013), we found that blackbirds and song thrush at our New Zealand study sites responded to the non-mimetic, fully black eggs with different behavioural modes of egg rejection: blackbirds typically deserted experimental clutches with black eggs, while song thrush typically ejected black eggs and continued to incubate the rest of the clutch (Fig. 3). The comparisons with the non-manipulated nests showed that only the blackbirds' response of higher nest desertion to the black egg treatment can be interpreted as a foreign-egg rejection behaviour in response to experimentally manipulated shell colours. In turn, behavioural outcomes in the other experimental treatments, including both treatments in the song thrush, showed no more desertions compared to the controls, implying that nest desertion is not a specific response to those specific types of eggshell colour manipulation in our study population of the song thrush (also see SAMAŠ et al. 2011).

The different modes of foreign-egg rejection responses reported here are likely to be behavioural tactics (i.e., plastic traits, and not fixed strategies, at the level of the individual: sensu GROSS 1996), because our prior work showed that active nests exposed to sequential experimental parasitism by the black painted egg, followed by the 20-spot treatment, showed ejection, followed by desertion, type of responses (IGIC et al. 2009; also see SAMAŠ et al. 2011). In addition, the results of our statistical analyses reject the hypothesis that differences in behavioural modes of egg rejection were owing to experimental or observational variation in year, site, reproductive stage, or seasonality, as neither of these predictors explained significant proportions of behavioural variability in our study taxa (Table 2).

Our findings are theoretically consistent with several scenarios for parasite virulence and the evolution of blackbird and song thrush anti-parasite egg-rejection behaviours. First, the pattern of greater likelihood of nest desertion over egg ejection in blackbirds, with the smaller clutch size, relative to song thrush, with the larger clutch size, is consistent with the predictions of the scenario that low-virulent parasitism has selected for the differences in the species-specific pattern of egg rejection tactics between blackbirds and song thrush (SERVEDIO & HAUBER 2006).

Second, life-history theory also predicts that any low-cost context that consistently reduces the breeding success of nesting birds (i.e., the presence of detritus, broken shells, foreign objects, etc., in the nest, TINBERGEN et al. 1962; HAUBER 2003c; GUIGUENO & SEALY 2009) selects for nest desertion by blackbirds in response to foreign objects in the nest, compared to song thrush because of their relative differences in clutch sizes (SERVEDIO & HAUBER 2006).

Third, egg rejection in blackbirds may have evolved in response to less virulent brood parasitism compared to more virulent parasitism in song thrush. For example, more frequent intraspecific brood parasitism in blackbirds versus more frequent cuckoo parasitism in song thrush would also predict the same alternative patterns of egg rejection behaviours that were documented in our study (SERVEDIO & HAUBER 2006). In contrast to this scenario, only rare instances of cuckoo parasitism have been recorded on any *Turdus* species in Europe (MØLLER 1976; MOKSNES & RØSKAFT 1995; GRIM et al. 2011).

Fourth, it is also possible that interspecific brood parasitism has less costly consequences for blackbirds than for song thrush, even when caused by otherwise typically virulent parasites. For example, cuckoo chicks do not always succeed in some host species' nests, owing to nest architecture, foraging regimes and nestling discrimination (KLEVEN et al. 1999; GRIM 2006b, 2006c; YANG et al. 2013). However, this scenario is rejected by available empirical data. Although experimentally introduced sole cuckoo chicks do not survive in nests of blackbirds (GRIM 2006a), they succeed in evicting all host progeny before they die, and would thus represent highly virulent parasitism in each parasitized brood (GRIM et al. 2011). In contrast, although sole cuckoo chicks grow rapidly and fledge successfully from nests of song thrush (GRIM 2006a), they die within a couple of days when sharing the nest with host chicks that they are unable to evict from deep song thrush nests, representing low cost parasitism (GRIM et al. 2011). Accordingly, cuckoo parasitism is potentially more virulent in nests of the blackbird compared to the song thrush, and so any interpretation of our song thrush egg rejection data in response to highly virulent, interspecific cuckoo parasitism, is not supported by these published empirical data. Moreover, recent evidence shows that *Turdus* thrushes are unsuitable hosts for cuckoos, due to thrush general life-history traits that are unrelated to parasitism per se (GRIM et al. 2011).

Thus, our data are most consistent with a role for less virulent type of brood parasitism, including low virulence typically caused by intraspecific brood parasitism (Pilz et al. 2005), in the evolution and maintenance of species differences in *Turdus* egg rejection behaviours. Future quantitative work should address not only the occurrence of intraspecific brood parasitism in blackbirds and song thrush (yes: GRIM & HONZA 2001; MOSKÁT et al. 2003; SAMAŠ et al. 2011, pers. obs.; no: CREIGHTON 2001; STREIF & RASA 2001), but also its relative prevalence and reproductive costs, within and outside the native ranges of these thrushes, using behavioural and genetic markers (LATIF et al. 2006; SEGELBACHER et al. 2008). Furthermore, given the parallel predictions of the alternative evolutionary scenarios involving both less virulent inter- and intraspecific parasitism, future experimental and comparative work should focus on predicting additional, critical differences in the egg rejection behaviours of *Turdus* species in response to more or less virulent inter- and intraspecific brood parasitism in host ranges sympatric or allopatric with interspecific brood parasites. For instance, there is now need for comparing regions of realized or potential (perceived risk, see WELBERGEN & DAVIES 2012) high vs low rates of intraspecific parasitism and comparing different *Turdus* species exposed to more vs less virulent interspecific brood parasites (e.g., parasitism by *Cuculus solitarius* in South Africa: HONZA et al. 2005 vs *Molothrus bonariensis* in South America: ASTIÉ & REBOREDA 2006). Finally, a comparative analysis of hosts' responses to varying costs of parasitism may also include an analysis of ecological and evolutionary variation and shifts in the clutch sizes of hosts between sympatry and allopatry and with historical exposure brood parasites with low or high virulence (see HAUBER 2003a).

Irrespective of the exact path of evolutionary history, our data confirm the suitability and value of life-history-informed modelling, together with experimental manipulations of the appearance of birds' own eggs. These approaches can be used to effectively assess alternative, though not necessarily mutually exclusive, evolutionary predictions including the diversity of sensory mechanisms (Honza et al. 2005; Moskát et al. 2008), the role of learning in parasite recognition (Hoover et al. 2006), the relative virulence of brood parasites (Servedio & Hauber 2006; this study) and shifts in optimal acceptance thresholds (Reeve 1989; Servedio & Lande 2003; Hauber et al. 2006; Moskát & Hauber 2007). In addition, this new work calls for further experimental work and analyses, using standardized methodologies, to compare and contrast the egg rejection behaviours of potential hosts within and outside the areas of sympatry with differently virulent avian brood parasites.

ACKNOWLEDGEMENTS

M.E. Hauber and P. Samaš contributed equally to this work. Permissions to access nesting sites were granted by private landowners and the Auckland Regional Council and local authorities in Finland. Our experiments were approved by the University of Auckland Animal Ethics Committee. For assistance and discussions we are grateful to R. Boulton, J. Briskie, M. Cherry, J. Dale, D. Dearborn, B. Gill, B. Igic, M. Herberstein, M. Honza, O. Krüger, C. Millar, C. Moskát and C. Spottiswoode. P. Cassey is an Australian Research Council (ARC) Future Fellow (FT0991420). Funding was provided by the Human Frontier Science Program RGY69/07 (to T. Grim, P. Cassey and M.E. Hauber) and RGY83/2012 (to M.E. Hauber and T. Grim). Earlier drafts of this manuscript also benefitted critically from referees' comments.

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